PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 45, No. 10, pp. 255–266, 5 figs., 2 tables. April 12, 1988

MARGINAL MARINE PLEISTOCENE FOSSILS FROM NEAR MOUTH OF MAD RIVER, NORTHERN CALIFORNIA

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Abstract: Late Pleistocene high-energy nearshore to strand-plain sands and gravels are succeeded by shelly backbar deposits in a cliff exposure near the mouth of Mad River, coastal Humboldt County. Backbar sediments consist of a protected slough-margin sandflat and an overlying muddy-bottom slough-basin facies. Fossil associations from both facies are dominated by mollusks (23 species in all), many of which are in place or only slightly disturbed. The association from the sandflat facies is dominated by balanid barnacles and infaunal suspension-feeding bivalves (*Saxidomus gigantea, Protothaca staminea, Tresus* sp.). Fine-grained slough-basin deposits contain remains of oyster gardens consisting of clumps of *Ostrea lurida* along with barnacles, the ectoparasitic snail *Odostomia nota*, and borings produced by the endolithic polychaete *Polydora* sp.; the intervening muddy matrix surrounding oyster clumps contains *P. staminea* and the infaunal deposit-feeding bivalve *Macoma nasuta*.

Received May 20, 1987. Accepted September 29, 1987.

Introduction

In January and February 1986, a series of winter storms caused coastal erosion in Humboldt County, California, with high water and extensive bank erosion along the lower reaches of the Mad River. The storms produced a new exposure of Pleistocene sediments in bluffs at the mouth of the river, located 1 km southwest of Arcata Airport (Fig. 1, 2). Near the top of the fresh exposure we found two fossiliferous beds containing many untransported shallow marine and estuarine mollusks. In this paper we describe the fossil deposits and relate them to original depositional environments and benthic communities.

This site is one of few low-energy late Pleistocene marine fossil localities in northern California, north of the type area of the Hookton Formation, consisting largely of well-preserved, autochthonous bivalve and gastropod shells. The excellent state of in situ preservation, with many infaunal and epifaunal-cemented bivalves still in life orientations, permits reconstruction of original community composition and structure, and the documentation of benthic ecology of Hookton (or Falor) Formation equivalents in the mouth of the Mad River area. We studied both the large, conspicuous mollusks typically reported in regional stratigraphic studies as well as diminutive species usually overlooked when isolated localities are sampled by merely hand-picking surface

FIGURE 1. Aerial photograph taken in 1984 showing the fossil locality and the following landmarks: (1) U.S. Highway 101; (2) Arcata Airport on the surface of Dows Prairie; (3) Widow White Creek; and (4) town of McKinleyville.

exposures. Accurate estimates of species richness and relative abundance of mollusks were achieved by bulk sampling at our study site.

Bulk sampling allows retrieval of small mollusks that are seldom mentioned in the paleontologic literature and are not well known from modern environments. These components of fossil deposits, although poorly known and sometimes difficult to determine to species (e.g., Pyramidellidae), should not be ignored. They were integral members of original benthic communities and may represent the only preserved evidence of biotic interactions such as parasitism. From a stratigraphic perspective, these smaller mollusks are untested as zonal guide fossils, taking into account the probability that many are restricted to particular sedimentary facies. They are essentially unexploited as stratigraphic guides, yet many occur in large numbers and could be sampled by subsurface methods.

Significantly, the two fossiliferous beds that we studied had sedimentologic and paleoecologic characteristics indicating deposition at or only slightly below paleo-sea level. In an area and time

FIGURE 2. Fossil locality as it appeared in March, 1986. The two fossiliferous beds are located at the level between white arrows; scale indicated by shovel, which is about 1.5 m long.

interval when tectonics, sediment supply, and glacio-eustatic fluctuations were producing rapidly changing, environmentally varied coastal landscapes, such marginal marine beds with their near-sea level biota of oysters and zosteracean plants are important indicators of former shoreline positions. Recognition of such deposits would be useful in studies of coastal uplift rates where an ancient sea level datum is required and age constraints are available.

LOCATION OF SITE AND METHODS

The exposure extends along the bluff line on the east bank of the Mad River, from 100 to 700 m north of the mouth of Widow White Creek along the seaward edge of Dows Prairie (Fig. 1; see also U.S.G.S. Arcata North 7.5′ topographic quadrangle). This lies within the Mad River Fault Zone, which was recently described by Carver (1985) as a northwest-trending zone of crustal

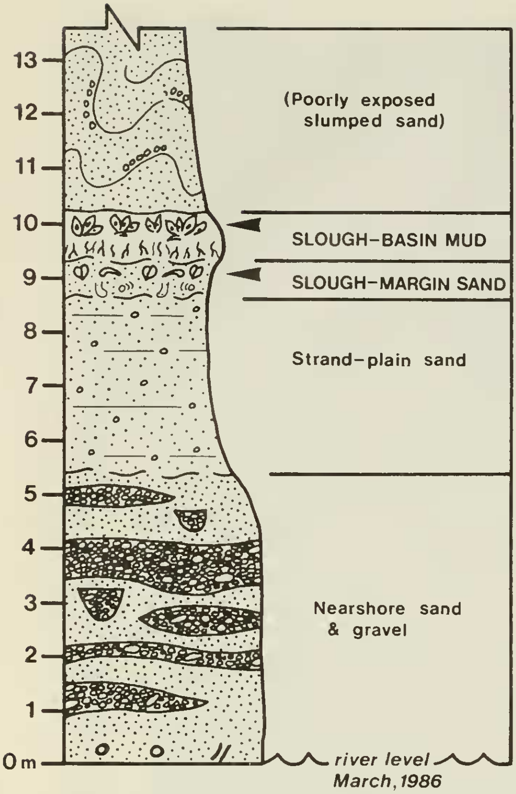

FIGURE 3. Stratigraphic section exposed at mouth of Mad River, showing levels from which samples were collected for paleoecologic analysis (arrows). Section extends upward for at least another 8 m, but is poorly exposed and disrupted by slumping.

compression, thrust faulting, and uplift resulting from convergence of the Gorda and North American plates. Our study site is bounded by the McKinleyville Fault to the north and by a splay of the Mad River Fault to the south (Carver 1985, Fig. 2). Thus, the fossil locality is situated within a fault block and elevation of fossiliferous beds is partly the result of structural uplift.

These two fossil beds occur at a height of between 8.5 and 10.5 m above the level of the river beach (Fig. 2, 3), which is roughly mean sea level (±1 m) near the mouth of the river. This is not the original elevation, however, owing to uplift and tilting of stratigraphic units in the fault zone. At the northern end of the outcrop, approaching the McKinleyville Fault, beds dip 4° to 8° south to southeast and strike generally east–west to northeast. Joints and small reverse faults are clearly visible here. Toward the center of the outcrop bedding gradually becomes horizontal. At the southern end, near Widow White Creek, slumping obscures bedding attitudes. In this area the mud bed shown in Figure 3 appears to be acting as a detachment surface and glide plane, above which the sediments are disrupted by slumping and fracturing.

We collected a total of eight 1-liter bulk samples: three from a bed interpreted as a backbar, slough-margin sandflat deposit and five from an overlying oyster-rich bed that represents a muddy-bottom, slough-basin deposit (Fig. 3). Each sample was soaked in 10% sodium hexametaphosphate solution and washed on a screen with 2-mm openings. All fossils separated from matrix were sorted, identified to species if possible, counted, and examined for epi- and endobionts. Sources consulted in the identification of specimens included: Dall and Bartsch 1909; Oldroyd 1927; Willett 1928; Fitch 1953; Abbott 1974; Keen and Coan 1974; Griffith 1975; Smith and Carlton 1975; Morris et al. 1980; Bernard 1982. Results are summarized in Tables 1 and 2. We noted sedimentary textures, physical and biogenic structures, and geometry of bedding units in the field in order to reconstruct the depositional history of the section.

STRATIGRAPHIC CONTEXT

REGIONAL SETTING.—The fossil locality is situated in the northern part of the Humboldt Basin, which contains a thick sequence of Late Cenozoic marine and coastal nonmarine sedimentary units (Ingle 1976). Thickness in onshore sections exceeds 3,500 m (Hopps and Horan 1983). The central part of this basin is a north–south-trending trough located on the submerged continental shelf between Cape Mendocino and the California–Oregon border (Hoskins and Griffiths 1971). On land, isolated outcrops of Late Cenozoic beds apparently related to the Humboldt Basin extend from the vicinity of Garberville, southern Humboldt County, to Crescent City in Del Norte County. In the well-known exposures at Centerville Beach and Scotia Bluffs, west-central Humboldt County, thick sections in the basin sequence have been divided into the following formal stratigraphic units, all but the last comprising the Wildcat Group (Ogle 1953): (1) upper Miocene Pullen Formation; (2) Pliocene Eel River Formation; (3) Plio-Pleistocene Rio Dell Formation; (4) Plio-Pleistocene Scotia

Table 1. Fossils from Sandflat Facies (See Fig. 3, 5).

Taxa	Average no. individuals/ liter sample* ($n = 3$)	Standard deviation	Type organism/substrate niche and feeding group†
Autochthonous components (intertidal to shallow subtidal sandy-bottom association)			
Balanus sp.	96.7‡	18.6	Ci/EPSF
Protothaca staminea (Conrad, 1837)	45.7‡	9.6	Bi/INSF
Tresus sp.	6.3	0.6	Bi/INSF
Turbonilla raymondi Dall and Bartsch, 1909	6.3	1.2	Ga/VAGP
Saxidomus gigantea (Deshayes, 1839)	5.0	2.0	Bi/INSF
Nutricola sp.§	4.7	1.2	Bi/INSF
Clinocardium nuttallii (Conrad, 1837)	2.0‡	1.0	Bi/INSF
Cryptomya californica (Conrad, 1837)	0.3	0.6	Bi/INSF
Transported components			
Ostrea lurida Carpenter, 1864	53.0	—	—
Mytilus edulis Linné, 1758	20.7	—	—
Macoma nasuta (Conrad, 1837)	6.7	—	—
Odostomia nota Dall and Bartsch, 1909	6.7	—	—
Cylichnella culcitella var. *eximia* (Baird, 1863)	4.0	—	—
Brachyura indet.	2.7	—	—
Mysella tumida (Carpenter, 1864)	1.3	—	—
Mopalia sp.	0.3	—	—
Cliona sp.	rare‖	—	—
Polydora sp.	rare	—	—

* For broken mollusk specimens: apex had to be present to count as one gastropod, beak to count as ½ bivalve.

† Type organism:

Bi	bivalve mollusk
Ga	gastropod
Pp	polyplacophoran
Ci	cirriped
Ma	malacostracan
An	annelid worm
Br	bryozoan
Pr	sponge
Vt	vertebrate
Pt	plant

Substrate niche and feeding group:

EPSF	epifaunal suspension-feeder
INSF	infaunal suspension-feeder
INDF	infaunal deposit-feeder
VAGP	vagrant ectoparasite
VAGC	vagrant carnivore or macrophagous scavenger
VAGG	vagrant grazer or microphagous scavenger
PP	primary producer

‡ Some specimens may have been transported from adjacent slough-basin (see Table 2).

§ Possibly extinct.

‖ Where counts of individuals were not possible (as with shell-boring organisms) the terms common, uncommon, and rare are used.

Bluffs Sandstone; (5) lower to middle Pleistocene Carlotta Formation; and (6) middle to upper Pleistocene Hookton Formation. Depositional environments and age relationships of these units were re-evaluted by Ingle (1976), Wagner (1980), Morrison and Sarna-Wojcicki (1981), and Sarna-Wojcicki et al. (1987).

Beginning roughly 500,000 yr B.P., Humboldt Basin deposits were subjected to tectonic compression directed from the northeast and southwest. This is reflected in the series of northwest-trending folds and thrust faults that extend across coastal Humboldt County (Carver 1985; Carver et al. 1986). Hookton Formation beds accumulated for the most part in downwarped areas within marginal marine and coastal alluvial plain settings after this deformation had begun. Ogle (1953) considered the Hookton separate from the Wildcat Group owing to its stratigraphic position above a regional angular unconformity. In most outcrops the formation consists of discontinuous sand beds, sandy conglomerate, thin interbeds or lenses of mud, and at least two volcanic ash layers. Mud interbeds in the type area south of Eureka often contain an *Ostrea–Saxidomus* invertebrate fauna like the one we describe from our study site. Where it has not been disrupted by faulting, the Hookton is an

TABLE 2. FOSSILS FROM SLOUGH-BASIN MUD FACIES (SEE FIG. 3, 5).

Taxa	Average no. individuals/ liter sample* ($n = 5$)	Standard deviation	Type organism/substrate niche and feeding group†
Autochthonous components (subtidal, muddy-bottom oyster garden association)			
Ostrea lurida Carpenter, 1864	119.0	44.5	Bi/EPSF
Odostomia nota Dall & Bartsch, 1909	32.0	11.4	Ga/VAGP
Balanus sp.	25.8‡	21.7	Ci/EPSF
Protothaca staminea (Conrad, 1837)	17.8	9.9	Bi/INSF
Bittium eschrichtii (Middendorff, 1849)	13.0	12.2	Ga/VAGG?
Mysella tumida (Carpenter, 1864)	3.4	1.5	Bi/EPSF?
Macoma nasuta (Conrad, 1837)	3.2	1.1	Bi/INDF
Nutricola sp.§	2.6	4.2	Bi/INSF
Mopalia sp.	2.4	1.5	Pp/VAGG
Mytilus edulis Linné, 1758	2.0	1.2	Bi/EPSF
Granulina margaritula (Carpenter, 1857)	0.8	0.8	Ga/VAGG?
Cylichnella culcitella var. *eximia* (Baird, 1863)	0.8	0.8	Ga/VAGC
Clinocardium nuttallii (Conrad, 1837)	0.8	0.8	Bi/INSF
Alvinia compacta (Carpenter, 1864)	0.6	0.9	Ga/VAGG?
Littorina scutulata Gould, 1849	0.6	0.9	Ga/VAGG
Brachyura indet.	0.4	0.5	Ma/VAGC
Polydora sp.	common‖	—	An/INSF
Cliona sp.	uncommon	—	Pr/INSF
Spathipora sp.	uncommon	—	Br/INSF
Zosteraceae indet.	uncommon	—	Pt/PP
Fish bones	rare	—	Vt/VAGC?
Transported components			
Saxidomus gigantea (Deshayes, 1839)	0.6	—	—
Hinnites giganteus (Gray, 1825)	0.2	—	—
?*Fissurella* sp.	0.2	—	—
?*Tricolia* sp.	0.2	—	—
Turbonilla raymondi Dall & Bartsch, 1909	0.2	—	—
Clypeastroida indet.	rare	—	—
From float only			
Diodora aspera (Rathke *in* Eschscholtz, 1833)		rare, transported	
Nassarius mendicus (Gould, 1849)		rare, autochthonous?	

Superscripts and abbreviations explained in footnotes of Table 1.

essentially flat-lying unit with beds dipping <5°. A maximum age of 700,000 and minimum age of 120,000 yr B.P. have been determined for the formation based on radiometric dating of volcanic ash and amino acid racemization analysis of *Saxidomus* shells (Kennedy 1978; Meyer et al. 1980; Wagner 1980).

We review the Hookton Formation at some length because the "pre-terrace" Quaternary deposits at the mouth of Mad River were previously included in this formation by Evenson (1959). Any formation assignment in this area is problematic because of faulting, lack of continuous exposures, and a dearth of unique lithologies or conspicuous marker beds. Our locality, however, could be within the Hookton Formation because of close resemblance to Hookton lithologies; mouth of Mad River deposits are largely unconsolidated sands and sandy gravels with subordinate muddy sediments of nearshore marine to estuarine origin. This lithologic correlation is supported by a virtual lack of deformation of beds at our site, except near a major fault, and fossil associations consisting almost exclusively of extant species. An alternative interpretation was made by Carver (1985), who mapped lower to middle Pleistocene Falor Formation deposits in stream valleys along the western edge of Dows Prairie, extending the unit to the coast from its type area near Maple Creek and Korbel, inland Humboldt County (see Manning and Ogle 1950). Carver (pers. comm., June 1986) argued that: (1) the term "Hookton Formation" should be used only in its type area near the mouth of Eel River, but it has questionable validity even there because it may not everywhere be separated from the Wildcat Group by a regional unconformity and may grade downward into upper Wildcat deposits; and (2) Hookton and Falor lithologies are identical, as far as anyone knows, and the term "Falor Formation" should be considered a senior synonym in the Mad River Fault Zone in any case. These units deserve more detailed study, and type and reference sections need to be established before firm lithostratigraphic correlations can be made.

In addition, Kohl (1974) used the informal designation "Crannell beds" for possibly coextensive Pleistocene deposits exposed near the mouth of Little River, 4 km north of our locality. Kohl's report is important for its complete checklist of fossils from the Crannell site. Roth (1979:77–79) discussed relationship of stratigraphy and fauna from this locality.

Mouth of Mad River Locality.—Sediments at our study site are mostly loose, olive brown, gravelly sands. The sand is medium to fine, moderately sorted, and subround to subangular. The only significant accumulation of silt–clay sediments is a thin, medium gray mud bed containing abundant oyster shells and plant fossils (Fig. 2, 3).

The local section begins at river level with a partially exposed unit of cross-bedded sand and gravel (Fig. 4a). Cross-stratification sets are trough- to wedge-shaped. Gravel occurs in lenticular beds, laterally continuous tabular beds, and as small channel-fill structures. Gravel beds are thicker near the bottom of the outcrop, and are normal-graded and trough cross-stratified internally. In the basal meter, rare *Ophiomorpha* burrows approximately 1 cm in diameter are located directly below a laterally continuous layer of planar-laminated, slightly muddy sand. Occasional flat lenses of peaty, silty sand also occur at this level. The assemblage of textures and structures suggests deposition in a high-energy nearshore marine setting, immediately seaward of a foreshore swash zone, which probably included the wave build-up and surf zone divisions described by Clifton et al. (1971). Thick, poorly graded gravel beds probably represent winter storm deposits, and rip currents may have formed the small gravel-filled channels (Leithold and Bourgeois 1984); cross-stratified sand and lenticular gravelly sand probably represent nearshore megaripples (Clifton et al. 1971). The laminated muddy sand and burrowed zone might indicate an interval of relatively low energy, or a slightly protected patch of seafloor buried and preserved by migrating megaripples. Abundance of cobbles and pebbles suggests proximity to a river mouth where coarse clastics were delivered directly into the ocean (David Miller, pers. comm., October 1986).

This high-energy facies grades upward into low-angle cross-stratified to planar-laminated sand. Texture of the sand fraction is similar to that of the underlying unit, but thick lenses and beds of gravel are lacking (Fig. 4b). This appears to be a strand-plain deposit formed in foreshore swash, beach platform, and overwash zones (Clifton 1969; Carter 1978; McCubbin 1982). Comparable environments can be seen in the modern strand-plain and spit complex located between the lower reaches of Mad River and the ocean (Fig. 1).

The strand-plain facies grades upward into a bed of burrow-mottled sand containing abundant bivalves usually in the upper 30–50 cm. Considering facies succession, bioturbate texture, and the presence of numerous infaunal bivalves in living positions within burrows (notably *Saxidomus* and *Tresus*), it appears that this unit was deposited in an intertidal to shallow subtidal, backbar sandflat bordering a protected slough.[1] Fossils from this facies are listed in Table 1.

Above the shelly sand, a conspicuous bed of gray mud contains slightly carbonized in situ eelgrass (Zosteraceae indet.) in the lower half and abundant *Ostrea* shells in the upper half. Blocks of this material have weathered out of the bluff face and occur at river level, in some places mixed with modern beach deposits (Fig. 4c). The mud with eelgrass fragments appears to be an intertidal to shallow subtidal mudflat deposit; the *Ostrea* bed represents oyster "gardens" that flourished in a shallow subtidal, muddy-bottom slough-basin. Fossils from the oyster-rich interval are listed in Table 2.

We did not study units above the stratigraphic level of the *Ostrea* bed. Generally, these consist

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[1] We use "slough" to mean a localized coastal depression or basin protected from the open ocean by a bay-mouth bar, but smaller and shallower than most lagoons or bays; this would include abandoned river channel segments, arms of larger lagoons, small pre-existing depressions that become flooded during high stands of sea level, and other, short-lived backbar estuarine settings of limited areal extent.

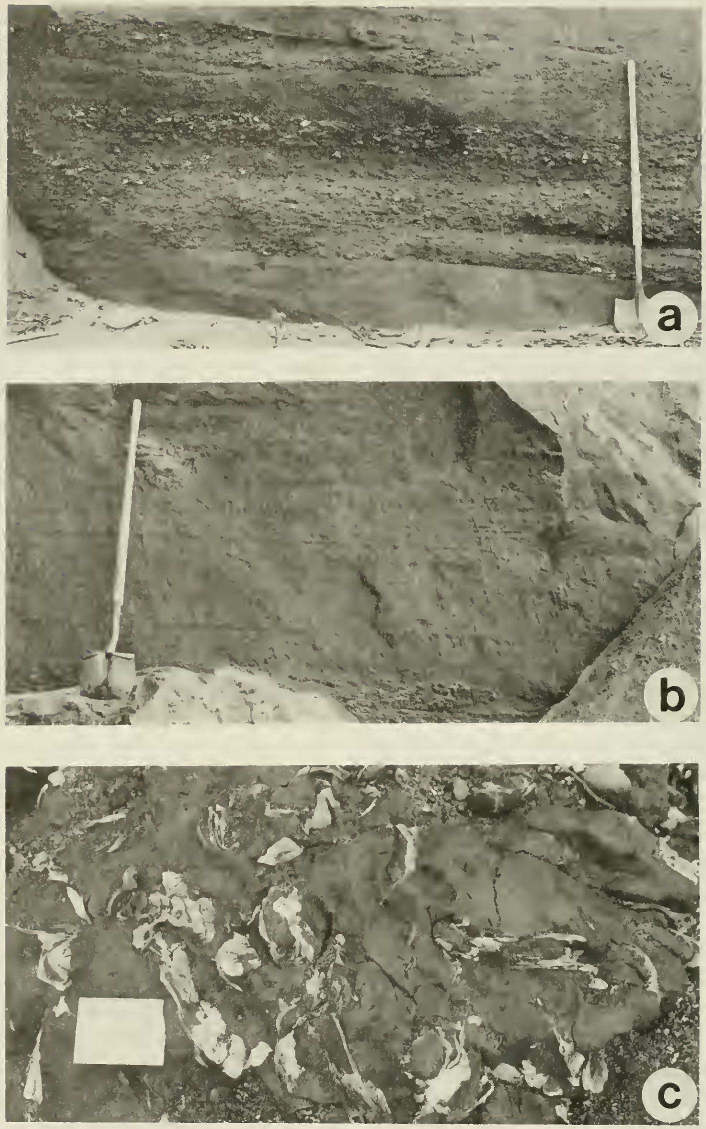

FIGURE 4. Close views of sediments and fossils: *a*, gravel beds in nearshore facies; *b*, horizontal to low-angle cross-stratified sand in strand-plain facies; *c*, boulder of slough-basin mud containing a clump of *Ostrea lurida*. Shovel in *a* and *b* is about 1.5 m long.

of pebbly sands that are covered by vegetation and slumped over subjacent beds along the bluff line.

The vertical transition from nearshore marine to backbar slough facies is a progradational sequence produced when a high-energy surf zone was replaced first by a barrier bar or spit (probably lacking extensive development of eolian deposits), and later by localized, short-lived paralic environments (see Carter 1978; Clifton 1982; McCubbin 1982). Such closely spaced, patchy, and rapidly changing depositional environments can be seen today along the coasts of northern California and Oregon, in segments between prominent rocky headlands where beaches are fully developed. In these areas of sediment accumulation, small lagoons or other types of estuarine basins with fringing marshes and sandflats are protected from the open ocean by emergent bay-mouth sand bars.

FOSSIL ASSOCIATIONS

Two distinctly different fossil associations (i.e., skeletal remains derived from a single, once-living community) were identified in multiple samples: (1) an intertidal to shallow subtidal sandy-bottom association, from the slough-margin sandflat facies (Table 1); and (2) a shallow subtidal muddy-bottom oyster garden association, from the slough-basin mud facies (Table 2). These were recognized by first separating autochthonous from transported shells, and then considering the preferred habitats of living representatives of the extant species (Smith and Carlton 1975; Morris et al. 1980; Ricketts et al. 1985). Transported shells were recognized by their abraded surfaces, fragmentation, and chalky or iron-stained appearance. Species interactions, such as parasitism and commensalism, were deduced by comparison with modern benthic communities and by noting infestations of epi- and endozoans. Both associations were dominated by bivalves and gastropods from a small shallow basin located landward of a strand-plain platform.

Samples from the sandflat deposit contained abundant balanid barnacles, occurring as disarticulated side plates, which in life probably covered the exposed surfaces of dead mollusk shells awash on the sandflat. Many of the dead shells utilized by *Balanus* sp. were *Ostrea lurida* derived from the adjacent slough-basin oyster clumps. Burrowing suspension-feeding clams, however, dominated the in-place fauna in terms of preserved biovolume and species richness (six of eight species). Among these, *Saxidomus gigantea* and *Tresus* sp. were found frequently in life orientations within burrows. Others, including *Protothaca staminea*, usually occurred as disarticulated valves and fragments. Presence of the commensal bivalve *Cryptomya californica* implies the presence of large, soft-bodied infauna such as echiurid worms and anomuran shrimps (Smith and Carlton 1975:130). The only gastropod that appeared to be in place was the minute pyramidellid *Turbonilla raymondi*, an ectoparasite with an unknown but probably infaunal host. Considering parasitic life habits of this small snail, its fragile shell, and the rigors of life on the sandflat surface, *T. raymondi* probably inhabited the burrow of its host. The list of indigenous species from the sandflat deposit is short and exclusive, with many organisms that either tolerated turbulence and exposure during tidal cycles (e.g., *Balanus*), or lived protected from periodic exposure well beneath the surface in burrows (e.g., *Saxidomus, Tresus*). Presence of large numbers of slow-burrowing *Protothaca* and bioturbate fabric of the bed indicate a fairly stable substratum rather than a constantly shifting sandy bottom. The original sandflat community is reconstructed in Figure 5a.

The oyster garden association differed sharply from the sandflat fauna in being dominated numerically by epibenthic mollusks (66.7% of individuals). Preserved biovolume was concentrated in *Ostrea lurida*, which occurred in isolated clumps surrounded by slightly shelly mud matrix (Fig. 4c). The oyster shells still displayed the original reddish-brown color mottles typical of the species (Hertlein 1959). Occurring with *O. lurida* were the following ecologic associates: (1) *Balanus* sp., exploiting abundant oyster clumps as islands of hard substrata on an otherwise uninhabitable muddy seafloor; (2) another pyramidellid snail, *Odostomia nota*, a likely ectoparasite on the oysters; and (3) a commensal or parasitic polychaete worm, *Polydora* sp., living in borings or embedments in oyster valves. Intervening muddy patches between oyster clumps were inhabited by infaunal bivalves, including *Protothaca staminea*, a suspension-feeder and ubiquitous species in both fossil associations, and *Macoma nasuta*, a deposit-feeder preferring protected muddy-bottom settings. Gastropod components, in addition to *O. nota*, consisted of *Bittium eschrichtii*, diminutive *Granulina margaritula*, and a probable microcarnivore, *Cylichnella culcitella* var. *eximia*—all of which have obscure ecologic roles in marginal marine communities. In addition, the association contained rare valves of the chiton *Mopalia* sp., which probably grazed green algae or diatoms from oyster shells. The indigenous fauna of the slough-basin mud facies totals at least 21 species representing perhaps the most complete and best preserved estuarine fossil association yet reported from late Pleistocene deposits of northern California. All trophic levels are represented to some extent, including primary producers (eelgrass), primary consumers (barnacles, bivalves, some gastropods), carnivores and scavengers (some gastropods and crabs), and parasites (pyramidellid snails). The original oyster garden community is reconstructed in Figure 5b.

Faunal transition in the mouth of the Mad

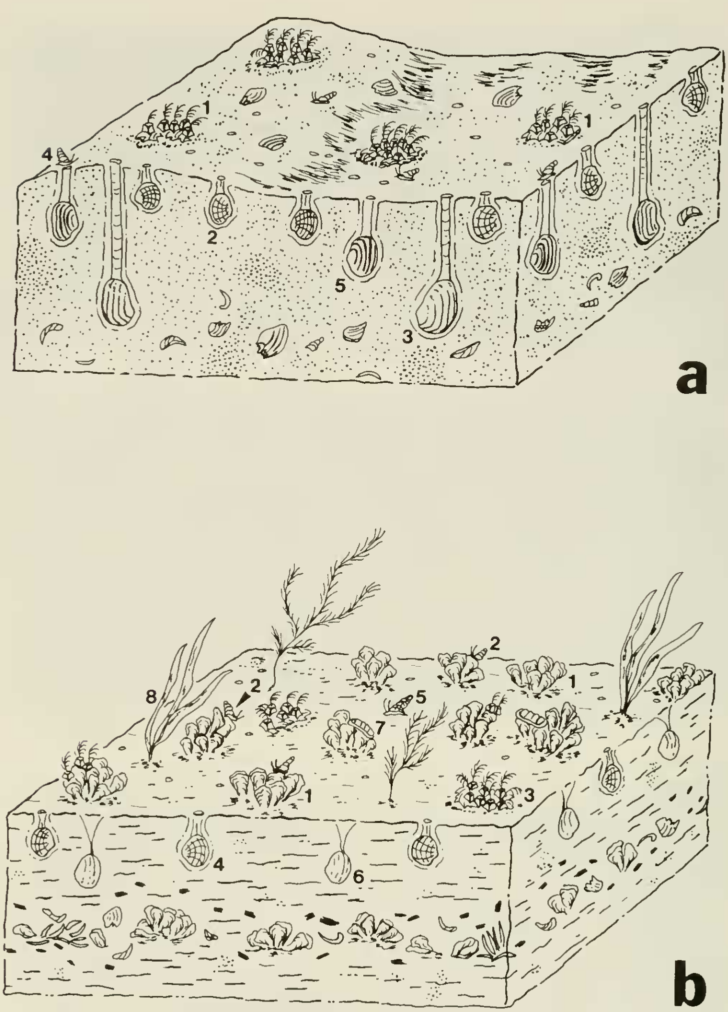

FIGURE 5. Reconstruction of benthic communities: *a*, sandflat community with (*1*) *Balanus* sp., (*2*) *Protothaca staminea*, (*3*) *Tresus* sp., (*4*) *Turbonilla raymondi*, and (*5*) *Saxidomus gigantea*; *b*, oyster garden community with (*1*) *Ostrea lurida*, (*2*) *Odostomia nota*, (*3*) *Balanus* sp., (*4*) *Protothaca staminea*, (*5*) *Bittium eschrichtii*, (*6*) *Macoma nasuta*, (*7*) *Mopalia* sp., and (*8*) eelgrass.

River section was the result of community replacement involving habitat alteration and species turnover (Miller 1986). This resulted when muddy sediments prograded over sandflat areas either as the slough-basin deepened and expanded in area or as protection from the open ocean became more complete at our site. Organisms responded to changes in substrate (from sand to mud), to reduced water turbulence and tidal exposure, and probably to changes in salinity fluctuations (Ricketts et al. 1985). The two original communities must have been situated adjacent to each other because large numbers of transported oyster valves were mixed with the sandflat fauna (Table 1) and the transition occurs within a thin (<1 m), continuous stratigraphic interval.

ACKNOWLEDGMENTS

We thank Raymond Burke, Gary Carver, and David Miller for background information on regional tectonics and sedimentology of our study site, and for comments on an earlier version of this paper. We also thank four anonymous reviewers for thorough evaluations that improved the quality of the final version. Frank Bernard helped us with identification of *Nutricola.* Nancy Walters processed bulk samples, Laura Leitch assisted with field work, and Camellia Armstrong and Carolyn Young typed drafts of the manuscript. Manuscript preparation was funded in part by Humboldt State University Foundation.

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